Global Change Biology (2003) **9,** 1465–1474

Solar UV-B decreases decomposition in herbaceous plant litter in Tierra del Fuego, Argentina: potential role of an altered decomposer community

VERÓNICA A. PANCOTTO*, OSVALDO E. SALA*, MARTA CABELLO†, NANCY I. LÓPEZ‡, T. MATTHEW ROBSON§, CARLOS L. BALLARÉ*, MARTYN M. CALDWELL§ and ANA L. SCOPEL*

*IFEVA, Facultad de Agronomía, Universidad de Buenos Aires and CONICET, Av. San Martín 4453 C1417DSE, Buenos Aires, Argentina, †Instituto de Botánica Spegazzini-UNLP, Calle 53, No. 477 B1900AVJ, La Plata, Argentina, ‡Departamento de Química Biológica, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón 2, Piso 4, Ciudad Universitaria, C1428EHA, Buenos Aires, Argentina, §The Ecology Center, Utah State University, Logan, UT 84322-5205, USA

Abstract

Tierra del Fuego, Argentina (55°S), receives increased solar ultraviolet-B radiation (UV-B) as a result of Antarctic stratospheric ozone depletion. We conducted a field study to examine direct and indirect effects of solar UV-B radiation on decomposition of *Gunnera magellanica*, a native perennial herb, and on the native community of decomposer organisms. In general, indirect effects of UV-B mostly occur due to changes in the chemical composition of litter, whereas direct effects during decomposition result from changes in decomposer organisms and/or differences in the photochemical breakdown of litter. We designed a full-factorial experiment using senescent leaves that had received either near-ambient or attenuated UV-B during growth. The leaves were distributed in litterbags and allowed to decompose under near-ambient or reduced solar UV-B during the growing season. We evaluated initial litter quality, mass loss, and nutrient release of decomposing litter, and microbial colonization of both initial litter and decomposed litter. We found that litter that decomposed under near-ambient UV-B had significantly less mass loss than litter that decomposed under reduced UV-B. The UV-B conditions received by plants during growth, which did not affect mass loss and nutrient composition of litter, affected fungal species composition but in different ways throughout the decomposition period. Before the decomposition trial, *Beauveria bassiana* and *Penicillium frequentans* were higher under reduced UV-B, whereas *Cladosporium herbarum* and pigmented bacteria were more common under the near-ambient compared to the reduced UV-B treatment. After the decomposition period, leaves that had grown under reduced UV-B showed higher frequency of *Penicillium thomii* and lower frequency of *Trichoderma polysporum* than leaves that had grown under near-ambient conditions. The UV-B condition received during decomposition also affected fungal colonization, with *Penicillium chrysogenum* being more frequent in leaves that had decomposed under reduced UV-B, while the other species were not affected. Our results demonstrate that, in this ecosystem, the effects of UV-B radiation on decomposition apparently occurred mostly through changes in the fungal community, while changes in photochemical breakdown appeared to be less important.

Keywords: decomposer community composition, decomposition, *Gunnera magellanica*, litter quality, ozone depletion, ultraviolet-B solar radiation

Received 20 March 2003; revised version received and accepted 2 May 2003

Correspondence: Osvaldo E. Sala, fax +54 11 45148730, e-mail: sala@ifeva.edu.ar

Introduction

Stratospheric ozone has decreased during the last two decades, particularly at high latitudes in the Southern

Hemisphere, resulting in enhanced penetration of ultraviolet-B radiation (UV-B, 280–315 nm) through the Earth's atmosphere (Madronich *et al*., 1998). The area of influence of the Antarctic 'ozone hole' frequently includes the southern part of South America during the spring (Frederick *et al*., 1994; Díaz *et al*., 1996). Within the ozone hole, 50% of the ozone can be depleted by the end of the winter, leading to large (i.e., 2×) increases in UV-B radiation at the ground level (Kirchhoff *et al*., 1997; Rousseaux *et al*., 1999). Apart from the direct influence of the Antarctic ozone hole, which is currently limited to periods of a few days during the spring, satellite data for Ushuaia (Tierra del Fuego, 55°S, Southern Argentina) indicate that a more general subtle, but steady, decline in the ozone column has taken place during the last two decades of the 20th century during all months of the growing season (October–March) (Rousseaux *et al*., 2001). Ground-level radiometric measurements obtained by the US National Science Foundation UV Radiation Monitoring Network in Ushuaia confirm that UV-B levels are substantially elevated relative to historic conditions (Díaz *et al*., 1996, 2000). Tierra del Fuego has a diverse flora and fauna compared with Antarctica and offers a unique opportunity to assess biological impacts of UV-B in terrestrial ecosystems in a system where ozone depletion has already occurred (Ballaré *et al*., 2001). Ozone depletion similar to, although less pronounced than, that observed over the Antarctic may occur over Arctic regions in the near future (Austin *et al*., 1992; Tabazadeh *et al*., 2000; Tolbert & Toon, 2001). Therefore, the study of the effects of ozone depletion in the Southern Hemisphere, while important in itself, also provides an opportunity to predict the potential consequences of increased UV-B in Northern Hemisphere ecosystems.

Decomposition of organic matter and nutrient mineralization from decaying litter is of considerable importance for ecosystem functioning. Decomposition rates are influenced by litter quality, species composition of decomposers, and environmental conditions (Swift *et al*., 1979; Coûteaux *et al*., 1995). A UV-B-induced alteration of decomposition could affect primary production, carbon storage, and carbon and nutrient fluxes between the soil and atmosphere (Zepp *et al*., 1998; Niemi *et al*., 2002). Litter decomposition may be affected directly or indirectly by UV-B radiation and may involve both biotic and abiotic processes. Direct biotic effects of UV-B can be exerted through changes in the species composition of decomposers. Direct abiotic effects can involve altered rates of photochemical breakdown of the litter. Indirect effects of UV-B, mediated by changes during growth and senescence of plants, can lead to differences in the chemistry and physical properties of the litter. These differences in litter chemical and physical properties may also modify the microbial community colonizing the litter.

Studies of the effects of UV-B on the decomposition of plant litter have shown a mixed response to increased UV-B, from which no general response pattern is discernable (Paul *et al*., 1999). Effects of UV-B (both direct and indirect) on chemical composition and mass loss have differed among species, ecosystems, and experimental approaches. Supplemental UV-B applied to plants with special UV lamps during growth (indirect effect) either decreased (Gehrke *et al*., 1995; Rozema *et al*., 1997), increased (Yue *et al*., 1998; Newsham *et al*., 1999; Cybulski III *et al*., 2000), or had no effect (Duguay & Klironomos, 2000; Verhoef *et al*., 2000) on decomposition rates. Direct UV-B effects on mass loss also depended on the plant species studied (Newsham *et al*., 1997; Rozema *et al*., 1997; Duguay & Klironomos, 2000; Moody *et al*., 2001). In each case, decomposer organisms were sensitive to UV-B, but their responses were variable among organisms (Gehrke *et al*., 1995; Newsham *et al*., 1997; Denward *et al*., 1999; Duguay & Klironomos, 2000). The lack of agreement on the overall effects of UV-B on decomposition may be due to at least three factors: (1) unrecognized patterns due to differences among species and ecosystems studied; (2) the manner in which UV-B was manipulated in the experiments; and (3) different responses at different UV-B fluxes. The two most common approaches to investigate the potential effects of ozone depletion on decomposition are exclusion of solar UV-B or supplementation of UV-B using UV lamps. Most of the studies were carried out in the Northern Hemisphere using lamp systems to simulate enhanced UV-B conditions. An unrealistic balance between UV-B, UV-A (315–400 nm), and visible (400–700 nm) radiation may exaggerate the effects of UV-B (Caldwell & Flint, 1997). The adoption of modulated lamp systems, which continuously measure incoming solar UV-B and adjust lamp output, has reduced this problem (Day, 2001). In our study, we tested the effects of current levels of solar UV-B radiation prevailing in Tierra del Fuego on decomposition. Our study compares current elevated UV-B levels vs. reduced levels in an attempt to assess the changes that already occurred on this ecosystem as a result of the erosion of the ozone layer and the consequent increase of UV-B.

We assessed both direct and indirect effects of UV-B radiation on decomposition, litter quality, nutrient release from the litter, and decomposer species composition in this terrestrial ecosystem. We carried out a factorial experiment with the litter of plants grown under reduced or near-ambient UV-B conditions by filtering existing solar radiation and litter that was

decomposed under reduced or near-ambient UV-B radiation. We evaluated litter quality, mass loss, and nutrient release from the litter, and species composition of decomposer community exposed to different UV-B treatments.

Materials and methods

Study site

The experiment was carried out in a native shrub community in the Tierra del Fuego National Park, Tierra del Fuego, Argentina (54°51′S, 68°35′W). The climate is sub-Antarctic with mean annual temperature of 5.6 °C and annual precipitation of 499 mm (Fuerza Aérea Argentina, 1986). The study site is located in an open area of a *Nothofagus* spp. deciduous forest and the community is dominated by the evergreen shrub *Chilliotrichum diffusum* (Forster f.) O. Kuntze, the creeping perennial herb *Gunnera magellanica* Lam. and the fern *Blechnum penna-marina* (Poiret) Kuhn (Moore, 1983).

Experimental design and UV-B manipulation

The experimental design was a 2×2 factorial using litter from plants grown under the two UV-B levels and then decomposed under the same two UV-B levels, reduced ($UV\text{-}B^{-}$) or near-ambient solar UV-B ($UV\text{-}B^{A}$) radiation. We manipulated the UV-B radiation received by plants during growth and of decaying litter during decomposition using plastic filters to achieve the different UV-B levels. Solar UV-B radiation was attenuated using 100-μm clear polyester (optically equivalent to 'Mylar-D', DuPont Co., Wilmington, DE, USA), which absorbs radiation below 310 nm but is transparent to longer wavelength radiation. We used a 38-μm Aclar plastic film (Aclar Fluoropolymer Film type 22A, Honeywell, Pottsville, PA, USA), transparent to nearly all solar radiation, including UV, to provide the near-ambient UV-B treatment. Filters were replaced when damaged or brittle, and were never used for more than 2.5 months, to avoid changes in optical properties due to photodegradation. Filters were perforated to let natural rainfall penetrate the experimental plots. Approximately 20% of the biologically effective solar UV-B, $UV\text{-}B_{be}$ (weighted using the generalized plant weighting function of Caldwell (1971)), passed through the perforated polyester (Mylar filters) and the perforated Aclar plastic allowed 90% transmission of the biologically effective UV-B (Searles *et al*., 1999). We measured soil water content in November and February using time-domain reflectrometry at 10 and 15 cm depth inside plots of each treatment (TDR, Time Domain Reflectometry, Trase System I, Soil Moisture Equipment Corp.). Soil water content was not significantly different ($P > 0.05$) in plots beneath the two types of filters.

Decomposition experiment

We collected freshly senesced leaves of *G. magellanica* grown during a whole season under near-ambient or reduced UV-B from the study site. We collected leaves from 10 different plots of each treatment. We sorted leaves from each treatment and air-dried them in paper bags at room temperature (20 °C) for 2 weeks. We filled litterbags, fiberglass 2-mm^2 mesh size ($10 \times 10\,cm^2$), with 2 g of senescent leaves and assembled them in a fully randomized design under both types of filters. Mesh bags partially block incoming UV-B, which may underestimate the direct UV-B effects, but we used the same mesh size in both treatments to minimize this problem. We kept 10 bags for analysis of the freshly collected litter. We dried the leaves at 65 °C for 48 h to convert air-dry mass into oven-dry mass.

We repeated the experiment twice: in 1999–2000 and 2000–2001. In the first experiment (Southern Hemisphere growing season 1999–2000), we placed a total number of 60 litterbags, 30 bags of litter from each growth treatment under 15 plots (replicates) from each decomposing treatment, i.e. each of the 15 plots received two bags, one from ambient UV-B litter and one from reduced UV-B litter. We placed them on November 12, 1999 and collected them on March 9, 2000 (4 months). In the second experiment (growing season 2000–2001), we placed a total number of 120 litterbags under 20 plots, i.e. each of 20 plots received four bags, two from ambient UV-B litter and two from reduced UV-B litter. We placed the bags on October 24, 2000, and collected 10 bags on December 11, 2000 and 20 bags on March 12, 2001 from each treatment (1.6 and 4.6 months, respectively).

Chemical analysis

We calculated dry mass loss and performed chemical analysis of initially collected and decomposed litter samples to evaluate litter quality and nutrient release from the litter. We estimated carbon, nitrogen, phosphorus, UV-B-absorbing compounds, cellulose, and lignin content before and after decomposition. At the end of the decomposition period, we weighed decomposed litter. We removed eight leaf fragments from each of five bags and placed them in plastic bags for microbial analysis. The remaining leaves of these bags were weighed fresh again and, as with the rest of the bags, were oven-dried at 65 °C for 48 h. We used oven-dried mass of litter to calculate water content and

extrapolated to total dry mass of those five bags prior to leaf removal.

We estimated the relative organic mass loss of litter at each sampling, correcting for inorganic content and soil contamination using dry combustion in a muffle furnace (500 °C for 4 h) to determine ash-free dry mass (AFDM). We used oven-dried litter for chemical analysis. We determined total organic carbon (C) as 50% of AFDM (Gallardo & Merino, 1993). We determined the content of UV-B-absorbing compounds in acidified methanol extracts. Approximately 0.02 g of senescent leaves were extracted in 3-mL methanol : HCl (99 : 1) for at least 48 h at − 20 °C and then we measured the absorbance in a spectrophotometer at 305 nm. UV-B-absorbing compounds were expressed as absorbance units (UA) per mg of dry mass diluted in 1 mL of extractant. We carried out total nitrogen (N) and phosphorus (P) determinations by a standard Kjeldahl acid-digestion procedure. We determined lignin content using the Van Soest acid-detergent method (Harmon & Lajtha, 1999). Nutrient release was calculated as the percentage of the original nutrient content remaining (Harmon *et al*., 1999):

$$\text{Nutrient release} = \frac{\%N_t \times \text{Mass}_t}{\%N_0 \times \text{Mass}_0}$$

where $\%N_t$ is the nutrient concentration at time t, mass_t the oven-dry mass at time t, $\%N_0$ the initial nutrient concentration, and mass_0 the initial oven-dry mass.

Decomposer community

During the second experiment (growing season 2000–2001), we analyzed microbial colonization of initial and decomposed litter. To study the fungal and bacterial colonization, we took a random sample of 8–10 leaves from each of five bags.

Fungal counts: We identified fungal species using the washing method of Parkinson and Williams (1961). We wetted leaf litter with sterile distilled water, and fragmented it in a mixer to a uniform size of 3–4 mm. We washed the fragments 10 times with sterile distilled water, draining the water between washings. We dried the particles for 24 h on filter paper to avoid bacterial and yeast growth after plating (Widden & Parkinson, 1973). Forty to fifty fragments per bag (four fragments per dish) were placed in Petri dishes on corn meal agar medium (CMA) inoculated with 0.5% sulfate streptomycin and 0.25% chloramphenicol, to avoid bacterial growth. We incubated the dishes at room temperature and examined them weekly during a 21-day period. We used Domsch *et al*. (1993) to identify sporulating fungi. We calculated the percent frequency of fungal species as the number of particles bearing a specific fungus/total number of particles × 100. Those particles that were contaminated or without colonies were not scored in the total number of particles.

Bacterial counts: We placed the leaves in 10-mL prechilled buffer (0.1 M potassium phosphate, pH = 7, 0.1% peptone) and removed bacterial cells from the leaves by 7-min sonication treatment in an ultrasonic bath. Aliquots (0.1 mL) were plated on King's medium B (King *et al*., 1954). We counted bacterial colonies on the diluted aliquots after 72 h of incubation at 30 °C. The number of bacteria was expressed per gram of dry mass diluted in 10 mL of buffer. We made individual counts for colonies appearing pigmented (yellow, orange, green, brown, or pink) and non-pigmented (white or cream) on King's medium B (KB).

Statistical analysis

To test the effects of reduced or near-ambient solar UV-B radiation on organic matter loss, we used a two-way analysis of variance (Sokal & Rohlf, 1981), with growth and decomposition conditions as the main factors. Differences in the chemical composition of plant material were assessed using Student's *t*-test or two-way ANOVA. The values were log-transformed if necessary to achieve normality. We tested the frequency of occurrence of fungal species using chi-square analysis (χ^2). Non-pigmented and total number of bacteria per gram of dry mass was transformed (natural logarithm) and we tested differences using two-way ANOVA. We used the Mann–Whitney *U*-test to compare the number of pigmented bacteria, as ANOVA assumptions were not achieved.

Results

Effects of UV-B on mass loss of litter

UV-B during decomposition on mass loss

Mass loss of *G. magellanica* was lower for leaves that decomposed under near-ambient UV-B than under reduced UV-B radiation (Fig. 1, left panels). After 1.6 months of decomposition, mass loss under near-ambient UV-B was 34% lower than under reduced UV-B conditions ($F = 10.91$, $P < 0.01$, data not shown), and after 4 and 4.6 months, mass loss was 14% and 26% lower, respectively, for the first and second experiments ($F = 10.20$ and 38.6, $P < 0.05$). We found no interactions between the effects of UV-B during decomposition (direct effects) and UV-B effects during growth and senescence of the plants (indirect effects) ($P > 0.05$), and consequently we report both effects separately.

UV-B during growth and senescence on mass loss

No indirect effect of UV-B on decomposition was observed. Exposure of *G. magellanica* leaves to reduced

or near-ambient UV-B radiation during growth and senescence did not modify the decomposition rate of the resulting leaf litter ($P > 0.05$, Fig. 1, right panels). We obtained the same result in both the first and second experiments.

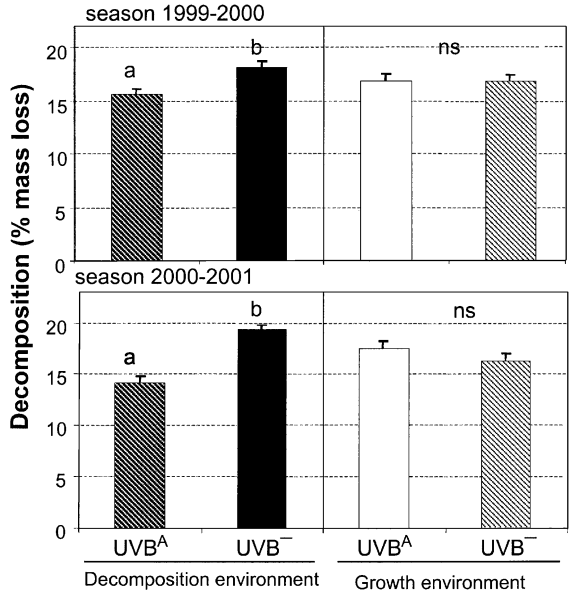

Fig. 1 Effects of UV-B on mass loss of litter. Relative mass loss of *G. magellanica*. Plants were grown under near-ambient (UV-B^A) or reduced ultraviolet-B radiation (UV-B^-) and decomposed under the same conditions in a 2×2 factorial experiment design. The two field experiments were carried out for (a) 4 months, season 1999–2000 ($N = 15$) and (b) 4.6 months, season 2000–2001 ($N = 20$). Each bar represents the mean and standard error of the mean, and different letters indicate significant differences among treatments at $P < 0.05$; ns indicates $P > 0.05$. Left panel: UV-B decomposition environment: mass loss of litter decomposed under near-ambient UV-B (UV-B^A) or reduced UV-B (UV-B^-). Right panel: growth environment: mass loss of litter from plants that grew under near-ambient UV-B (UV-B^A) or reduced UV-B (UV-B^-).

Effects of UV-B on nutrient content

UV-B during growth and senescence on litter quality and nutrient release

Before decomposition, initial litter quality was not affected by UV-B during growth. Total nitrogen, phosphorus, UV-B-absorbing compounds, and fiber content did not differ ($P > 0.05$) between the UV-B treatments received during growth (Table 1). The same result was observed after 4 and 4.6 months of decomposition (in the first and second years, respectively). There were no differences in the chemical content and nutrient release of litter of *G. magellanica* that grew under near-ambient or reduced UV-B treatments ($P > 0.05$, Tables 2 and 4).

UV-B during decomposition on chemical content and nutrient release

At the end of the decomposition period, the total nitrogen and phosphorus content of *G. magellanica* leaves was lower when litter had been decomposed under near-ambient UV-B conditions ($P < 0.05$, Table 3). However, the UV-B treatment received during decomposition had no effect on nutrient release of nitrogen or phosphorus over the course of decomposition ($P > 0.05$, Table 4). The percentages of lignin, cellulose, and UV-B-absorbing compounds were not significantly affected by UV-B ($P > 0.05$, Table 3). The C : N ratio of litter decomposed under near-ambient UV-B conditions was significantly higher than that observed under reduced UV-B conditions ($P < 0.05$, Table 3).

Table 1 UV-B effects during growth and senescence on initial litter quality

	First experiment			Second experiment		
Growing environment	UV-B^A	UV-B^-		UV-B^A	UV-B^-	
Nitrogen (%)	3.0 (0.1)	3.0 (0.2)	ns	3.2 (0.1)	3.1 (0.2)	ns
Phosphorus (%)	0.08 (0.01)	0.08 (0.01)	ns	0.09 (0.01)	0.08 (0.01)	ns
C : N	15.9 (0.3)	16.0 (0.9)	ns	15.3 (0.6)	15.6 (0.9)	ns
Lignin (%)	6.4 (0.6)	6.5 (0.9)	ns	6.6 (0.75)	6.9 (0.8)	ns
Cellulose (%)	18.8 (0.4)	17.9 (1.3)	ns	16.4 (1.6)	16.6 (1.3)	ns
UV-B-absorbing compounds (AU)	–	–		0.82 (0.15)	0.93 (0.16)	ns

Relative concentrations of nitrogen, phosphorus, lignin, cellulose, and absorbance units (AU) of UV-B-absorbing compounds per unit dry mass of *G. magellanica* leaf litter before decomposition. The values are the percentage of chemical compounds in dry mass of leaf litter grown under near-ambient (UV-B^A) or reduced ultraviolet-B radiation (UV-B^-). The plants grew during the austral growing seasons (September–March) of 1998–1999 (first experiment) and 1999–2000 (second experiment). Means and standard deviations are presented. The statistical significance of effects of UV-B on litter quality was tested with a Student's *t*-test comparing UV-B^A and UV-B^-. ns: $P > 0.05$.

Table 2 Effects of UV-B during growth and senescence on chemical composition at the end of the decomposition experiment

	First experiment			Second experiment		
Growing environment	UV-B^A	UV-B$^-$		UV-B^A	UV-B$^-$	
Nitrogen (%)	3.2 (0.2)	3.3 (0.3)	ns	3.8 (0.3)	3.7 (0.2)	ns
Phosphorus (%)	0.09 (0.01)	0.08 (0.01)	ns	0.10 (0.01)	0.10 (0.01)	ns
C : N	14.8 (1.0)	14.6 (1.2)	ns	12.9 (0.9)	13.2 (0.8)	ns
Lignin (%)	–	–		9.7 (1.6)	9.3 (2.1)	ns
Cellulose (%)	–	–		16.9 (1.1)	15.8 (1.9)	ns
UV-B-absorbing compounds (AU)	–	–		1.18 (0.29)	1.26 (0.27)	ns

Mean values and standard deviations of percentage nitrogen, phosphorus, lignin, cellulose, and absorbance units (AU) of UV-B-absorbing compounds per dry mass of *G. magellanica* leaf litter. Each value represents, the mean of the replicates grown under the same growth environment, and decomposed under both decomposition environments, for 4 and 4.6 months (first and second experiments, respectively). The first experiment was carried out during the growing season 1999–2000 and the second experiment was carried out during 2000–2001. UV-B^A: plants that grew under near-ambient UV-B, UV-B$^-$: plants that grew under reduced UV-B. ns: $P > 0.05$.

Table 3 Effects of UV-B during decomposition on chemical composition at the end of the decomposition experiment

	First experiment			Second experiment		
Decomposing environment	UV-B^A	UV-B$^-$		UV-B^A	UV-B$^-$	
Nitrogen (%)	3.3 (0.2)	3.5 (0.1)	**	3.6 (0.2)	3.9 (0.2)	**
Phosphorus (%)	0.09 (0.01)	0.09 (0.02)	ns	0.09 (0.00)	0.10 (0.01)	**
C : N	14.7 (1.0)	13.9 (0.4)	**	13.5 (0.7)	12.7 (0.7)	**
Lignin (%)	–	–		10.0 (2.0)	9.1 (1.6)	ns
Cellulose (%)	–	–		16.1 (2.0)	16.7 (1.0)	ns
UV-B absorbing compounds (AU)	–	–		1.25 (0.27)	1.19 (0.30)	ns

Percentage nitrogen, phosphorus, lignin, cellulose, and absorbance units (AU) of UV-B absorbing compounds per dry mass of *G. magellanica* litter decomposed under near-ambient UV-B (UV-B^A) or reduced UV-B (UV-B$^-$). Values are the means and standard deviations of litter grown under both treatments and decomposed under UV-B^A or UV-B$^-$ conditions. ns: $P > 0.05$, $^*P < 0.05$ and $^{**}P < 0.01$. For more details, see text and Table 2.

Table 4 UV-B effects during growth and senescence and during decomposition on nutrient release

	First experiment						Second experiment					
	Growing environment			Decomposing environment			Growing environment			Decomposing environment		
	UV-B^A	UV-B$^-$		UV-B^A	UV-B$^-$		UV-B^A	UVB$^-$		UV-B^A	UV-B$^-$	
Nitrogen remaining (%)	93.7 (6.7)	95.2 (3.5)	ns	93.5 (5.3)	95.4 (5.4)	ns	99.3 (5.3)	100.0 (4.3)	ns	100.0 (3.4)	99.0 (5.6)	ns
Phosphorus remaining (%)	94.4 (18.5)	95.1 (10.5)	ns	93.6 (11.2)	95.8 (18.0)	ns	94.7 (6.6)	98.0 (6.4)	ns	97.7 (5.8)	95.4 (7.2)	ns

Relative nitrogen and phosphorus remaining after 4 and 4.6 months of decomposition period (first and second experiments, respectively). The values are the percentage and the standard deviation of the original nutrient concentrations remaining at the end of the decomposition period. This was tested both for the UV-B treatment received during growth and senescence (growing environment) and during decomposition (decomposing environment) under near-ambient UV-B (UV-B^A) or reduced UV-B (UV-B$^-$). ns: $P > 0.05$. For more details, see Tables 2 and 3.

Effects of UV-B on decomposers

UV-B during growth and senescence on decomposers

Fungi: Before decomposition, the frequency of *Cladosporium herbarum* was higher in fragments of leaves that grew under near-ambient UV-B ($\chi^2 = 3.77$, $P < 0.05$; Fig. 2a). The opposite was observed for *Beauveria bassiana* and *Penicillium frequentans* ($\chi^2 = 4.48$ and 3.77, respectively, $P < 0.05$). In spite of the observed differences in fungal species composition of initial litter, we did not observe differences in litter quality, nor differences in mass loss due to UV-B during growth. After 4.6 months of decomposition, the environment where plants had grown affected the frequencies of *Penicillium thomii* and *Trichoderma polysporum* ($\chi^2 = 4.65$ and 3.85, $P < 0.05$; Fig. 2b). Plants that grew under near-ambient UV-B had a lower frequency of *P. thomii* and a higher frequency of *T. polysporum*. These trends were the opposite of those observed in colonization of litter before decomposition ($P > 0.05$, Fig. 2a). The proportion of uncolonized particles was low, ranging between 3% and 6% of the total number of particles for reduced and near-ambient UV-B treatments, respectively, and there were no statistically significant differences ($P > 0.05$) between treatments in this attribute.

Bacteria: Before decomposition, the number of pigmented bacteria was higher in fragments of litter grown under near-ambient UV-B ($U = 15$, $Z = 2.99$, $P < 0.05$) (Fig. 3a, right panel); however, colonization by pigmented bacteria was unaffected after 4.6 months of

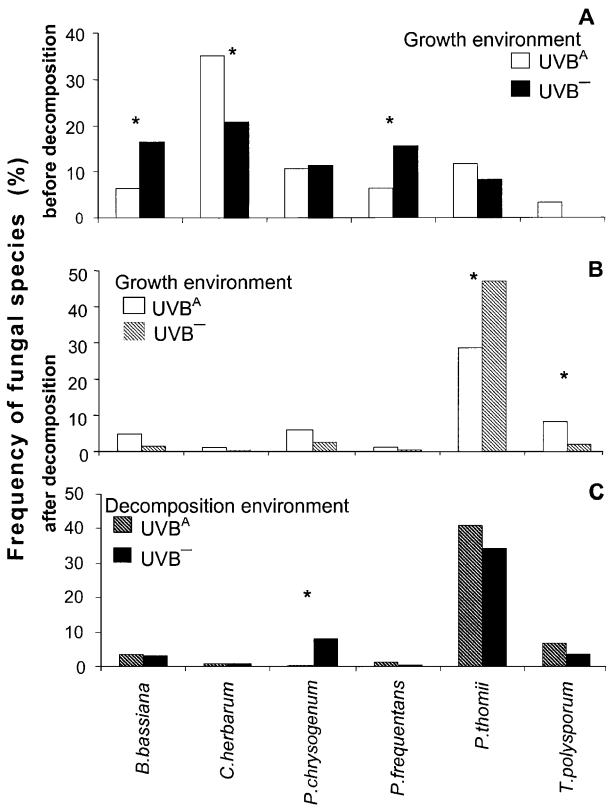

Fig. 2 Effects of UV-B on decomposer fungal species. Frequency of *B. bassiana, C. herbarum, P. chrysogenum, P. frequentans, P. thomii, and T. polysporum* on *G. magellanica* leaf litter: (a) fungal colonization of initial litter (before decomposition trial) under near-ambient UV-B (UV-B^A) and reduced UV-B (UV-B$^-$) ($N = 10$); (b) fungal colonization after 4.6 months of decomposition of litter from plants that grew under near-ambient UV-B (UV-B^A) or reduced UV-B (UV-B$^-$) and decomposed under both decomposing environments ($N = 5$); (c) fungal colonization after 4.6 months of decomposition of litter decomposed under near-ambient UV-B (UV-B^A) or reduced UV-B (UV-B$^-$) and grown under both growing treatments ($N = 5$). Bars represent the mean of the frequency of each species (number of fragments colonized by the species/number of total fragments by replicate). *Indicates significant differences at $P < 0.05$.

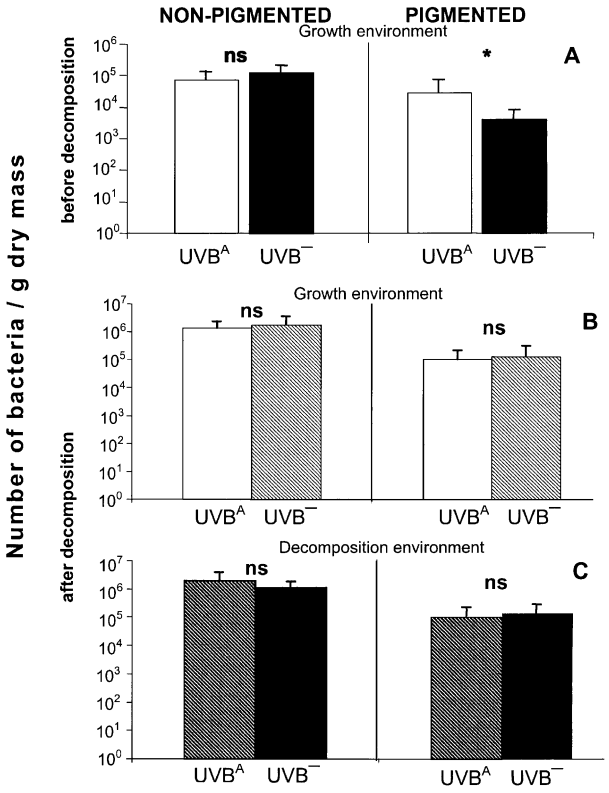

Fig. 3 Effects of UV-B on bacteria. Number of non-pigmented (left panel) and pigmented (right panel) bacteria per unit dry mass of *G. magellanica* litter: (a) colonization of initial litter (before decomposition); (b) colonization after 4.6 months of decomposition of litter from plants grown under near-ambient UV-B (UV-B^A) or reduced UV-B (UV-B$^-$) and decomposed under both decomposing environments; (c) colonization after 4.6 months of decomposition of litter that decomposed under near-ambient UV-B (UV-B^A) or reduced UV-B (UV-B$^-$) and grown under both growing treatments. Data are shown in logarithmic scale. *Indicates significant differences at $P < 0.05$.

decomposition (Fig. 3b, right panel). The number of non-pigmented bacteria both before and after 4.6 months was not different between UV-B treatments (Fig. 3a,b, left panel).

UV-B during decomposition on decomposers

Fungi: The decomposition UV-B environment affected the species composition of fungi. After 4.6 months of decomposition, *Penicillium chrysogenum* was significantly less common on leaves decomposed under near-ambient UV-B compared to reduced UV-B radiation ($\chi^2 = 7.38$, $P < 0.05$) (Fig. 2c). *P. thomii* and *T. polysporum* showed no effect of the UV-B environment during decomposition.

Bacteria: We were unable to detect significant differences in the number of pigmented or non-pigmented bacteria that colonized both treatments after 4.6 months of decomposition (Fig. 3c).

Discussion

The exposure of *G. magellanica* litter to different levels of solar UV-B radiation during decomposition caused significant changes in mass loss, chemical composition, and abundance of fungi. In both years of the experiment, near-ambient UV-B decreased the rate of litter decomposition compared to the reduced UV-B conditions. Direct effects of solar near-ambient UV-B on decomposers were apparently more important than any acceleration of photochemical breakdown by the higher flux of UV-B. Whereas the relative nitrogen and phosphorus concentration in the litter significantly increased in the reduced UV-B treatment during decomposition, nutrient release during decomposition did not. This suggests that the changes in nutrient concentration were largely driven by the observed changes in mass loss. The C : N ratios decreased with time and were higher under near-ambient UV-B than under reduced UV-B, which is in agreement with the lower decomposition rate under the higher UV-B treatment. Similar to our findings, Newsham *et al.* (1997) reported that oak leaves exposed to elevated UV-B radiation decomposed less rapidly than controls after 11 weeks. However, our results differ from some previous studies that reported increased decomposition under enhanced UV-B, and this was thought to be the result of increased photochemical breakdown of litter (Gehrke *et al.*, 1995; Rozema *et al.*, 1997). These two studies were conducted in the Northern Hemisphere with lamps that supplemented UV-B radiation. The UV-B doses on those plots ranged between 7.5 and 10 $kJ\,m^{-2}\,day^{-1}$ of biologically effective UV-B (Caldwell, 1971). These were considerably higher fluxes than those received in our site under near-ambient UV-B treatment, (about 3.8 and 3.0 $kJ\,m^{-2}\,day^{-1}$ for the first and second experiments, respectively, based on data from the NSF UV Monitoring Network). Perhaps, acceleration of photochemical litter breakdown is only detectable at higher UV-B than those occurring in ambient solar radiation in Tierra del Fuego. At higher UV-B fluxes from lamps, the increased photochemical breakdown might have overshadowed other processes leading to decreased decomposition rate, such as effects on microbes colonizing the litter.

The only apparent results of exposing plants to different UV-B conditions during growth were changes in bacterial and fungal colonization of litter before decomposition. There were no changes in litter quality based on the chemical characteristics measured. However, there may have been other chemical or morphological changes not measured that could have affected decomposers and, therefore, decomposition. Initial colonization by pigmented bacteria and the fungus *C. herbarum* was higher on initial litter from plants grown under near-ambient UV-B. Pigmented species such as *C. herbarum* may better tolerate higher levels of UV-B radiation, due to the protection conferred by UV-B absorbing pigments (Durrell & Shields, 1960). For example, pigments are effective in protecting *Escherichia coli* (Sandmann *et al.*, 1998), cyanobacteria (Ehling-Schulz *et al.*, 1997), and fungi (Moody *et al.*, 1999; Duguay & Klironomos, 2000) from UV-B radiation. Also, initial colonizations of *B. bassiana* and *P. frequentans* were higher under the reduced UV-B treatment. Similarly, survival of *B. bassiana* on wheat-grass leaves and abundance of *P. frequentans* in a bog were higher in the lower UV-B treatment (Inglis *et al.*, 1995; T.M. Robson, unpublished data).

Exposure of plants to near-ambient UV-B radiation during growth led to a significant decrease in the abundance of *P. thomii* and an increase in *T. polysporum* by the end of the decomposition period. Seasonal fluctuations may account for the higher frequency of these fungi at the end of the decomposition period in comparison with the initial colonization (Godeas, 1983). We found a clear influence of UV-B on the fungal community; however, all the mechanisms by which UV-B alters the decomposer community are not known (Paul & Gwynn-Jones, 2003). Decreased frequency of some fungal species under higher UV-B may have resulted from direct damage to these species and increased frequency of other fungal species under the higher UV-B may have been due to competitive release by the decreased frequency of UV-B-damaged species. We do not know if these changes in the decomposer community are entirely responsible for the large differences in mass loss of litter during decomposition under the two UV-B treatments.

Our study demonstrates changes in the initial stages of the decomposition process due to exposure to different UV-B conditions. If these large differences in mass loss due to UV-B treatments persist for the entire decomposition process, there could be substantial implications for the processing of carbon, nutrient mineralization, and carbon storage in the ecosystem (Swift *et al*., 1979). In the short term, a reduction of the decomposition rate resulting from enhanced UV-B may result in increased C-storage in the ecosystem. In the long term, the UV-B-induced reduction in decomposition and nutrient mineralization may constrain primary production and C input into the ecosystem, which may negatively affect C-storage. To date, our 6-year study of solar UV-B manipulation has not shown changes in primary production, carbon stocks, or mineral N and P concentrations in the soil (V. Pancotto, unpublished data). Studies of greater duration may be necessary to detect indirect ecosystem effects of UV-B and to test for different steady-state carbon stocks. Thus far, we have been able to detect a substantial reduction of C losses, apparently mediated by changes in the decomposer organisms, which have the shortest life span and potentially the fastest rate of change.

Acknowledgements

We thank A.T. Austin and C. Giordano for valuable comments on the manuscript. We thank R. Saenz Samaniego, N. Garibaldi, and M. Tagliazucchi for field and laboratory assistance, C. Giordano who helped with the UV-absorbing compounds analysis, and C. Rousseaux who made a number of helpful suggestions on the project. We thank the staff of the Centro Austral de Investigaciones Científicas (CADIC-CONICET) who offered logistical support in Tierra del Fuego especially E. Olivero and S. Díaz. We thank Administración Parques Nacionales (APN) for their permission to work in the Tierra del Fuego National Park. This research was supported by the US National Science Foundation (NSF-Grant Numbers 95-24144 and 98-14357), the Inter American Institute for Global Change Research (CRN-012), Agencia Nacional de Promoción Científica y Técnica (ANPCyT), University of Buenos Aires (UBA), and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). O.E.S., N.I.L., C.L.B., and A.L.S. are career investigators from CONICET; M.C. is a career investigator from CIC.

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